

## INTERSPECIFIC INTERACTIONS BETWEEN WOOD-ROTTING FUNGI FROM OLD STANDING TREES

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**ABSTRACT** - Mycelial interactions between wood-rotting fungi isolated from old standing trees of peach and willow and from detached wood of willow, were studied on culture media. The outcome of all pairings between fungi from peach (*Coriolus versicolor*, *Pycnoporus sanguineus*, *Phellinus pomaceus*) were deadlock, whilst replacement of one species by the other characterized the interactions between fungi from willow (*Laetiporus sulphureus*, *Pycnoporus sanguineus*, *Panus tigrinus*, *Trametes extenuata*). During the replacement interactions the overgrowing species changed their mode of growth, whilst the replaced species exhibited morphogenetic, cytological and biochemical responses implying activation of senescent development. Pigmented zones always developed at the interface between paired cultures in deadlock and in replacement.

Diffusible metabolites produced by individual fungi and transmissible through ■ cellophane membrane had little effect on radial extension of the other fungi. However, in one case morphogenetic changes were induced which were maintained when submerged mycelium was transferred to fresh medium.

Deadlock responses between the species from peach could reflect partitioning in use of resources allowing the species to persist adjacent to one another. Conversely, the ecological strategy of fungi from willow was to take over domain where *Laetiporus sulphureus* had become established in the standing tree.

**RÉSUMÉ** - Les interactions entre mycélium de champignons causant la pourriture du bois de pêcher et de saule sur pied et de branches de saule coupées ont été étudiées en culture. Les résultats des confrontations entre champignons isolés de pêcher (*Coriolus versicolor*, *Pycnoporus sanguineus* et *Phellinus pomaceus*) montrent le blocage réciproque des colonies tandis que les champignons isolés de saule (*Laetiporus sulphureus*, *Pycnoporus sanguineus*, *Panus tigrinus* et *Trametes extenuata*) montrent le recouvrement d'une espèce par l'autre. Dans ce dernier cas, l'espèce recouvrante change de mode de croissance et l'espèce recouverte montre des transformations morphogénétiques, cytologiques et biochimiques conduisant à la sénescence. Une zone pigmentée s'observe toujours ■ l'interface entre les deux colonies.

Les métabolites diffusibles à travers la cellophane, produits par chaque espèce, ont un effet limité sur les champignons testés. Cependant, dans un cas, un changement morphogénétique est induit dans le mycélium immergé. Il se montre stable après plusieurs repiquages.

Le blocage réciproque observé entre espèces isolées du pêcher pourrait traduire le partage des ressources nutritives permettant aux espèces de coexister. Par contre, les champignons isolés de saule manifestent un envahissement du substrat après la colonisation préliminaire par *L. sulphureus*.

**KEY WORDS** : wood-rotting fungi, interspecific interactions, willow brown-rot, peach white-rot.

## INTRODUCTION

A large amount of literature (Mercer, 1982; Merrill & Shigo, 1979; Rayner *et al.*, 1987; Rayner & Coates, 1987; Shigo, 1967, 1972, 1979; Shigo & Marx, 1977) suggests that fungal decay of stem and branches of standing trees is initiated by wounds which allow access of non-decay-causing microorganisms prior to establishment of decay causing Basidiomycetes. However, it is becoming apparent that colonization in natural conditions occurs not necessarily by major wounds and when studying attached oak branches it was found that wood-rotting Basidiomycetes were primary colonizers (Boddy *et al.*, 1985, 1987; Boddy & Rayner, 1982, 1983a). Factors such as temperature, CO<sub>2</sub>, water activity, inoculum potential and interspecific interactions may all selectively influence which species of wood-rotting fungi succeed eventually in colonizing a specific resource (Boddy *et al.*, 1987; Clarke *et al.*, 1980; Rayner, 1986).

Changes in composition of a wood-rotting Basidiomycetes community may occur in relation with changes in the microenvironmental conditions which alter the competitive ability of one fungus in relation to the other. On the other hand, under the same conditions one species might shift its resource capture strategy according to the potential strategy of the other species with which it interacts (Rayner *et al.*, 1987). Mycelial senescence and changes of mode of growth of one or both of interacting fungi seems to be a common expression of mutual recognition (Rayner & Boddy, 1988).

As it seems that the interaction of wood rotting-fungi in culture media commonly reflects their ecological strategy in nature (Rayner *et al.*, 1987; Rayner & Boddy, 1988). The aim of this work was to determine how such interactions, between species colonizing old standing trees of willow and peach are correlated with observations in the distribution of their fruit-bodies. The role of diffusible metabolites during these interactions was also analysed.

## METHODS

### Sampling of fungi from natural communities

Large fruit-bodies of *Laetiporus sulphureus* (Bull.: Fr.) Murr. which had developed on the trunks of old standing willows (*Salix humboldtiana* Willd.) with large brown rotted areas were collected during several years. Some large branches (15-20cm diameter) of one tree apparently not colonized, were cut off in the autumn 1985 and staked horizontally. In some of them a few small fruit-bodies of *L. sulphureus* appeared on the proximal side of the branch, during next summer (1986). Close to the mid portion of these branches some basidiomes of *Panus tigrinus* Bull.: Fr.) Sing. developed one year later during the autumn (1987). Finally, abundant fruit-bodies of *Trametes extenuata* (Dur.: Mont.) Pat. emerged during the autumn of the following two year particularly from the cambial regions adjacent to the cut distal surfaces. On the other branches, several fruit-bodies of *T. extenuata* (in the distal part) and *P. tigrinus* (in the mid) developed initially (1987) and were superseded during the two following years by abundant fruit-bodies of *Pycnoporus sanguineus* (L. G. Meyer. Fr.) Murr.

At the same time, fruit bodies of *Phellinus pomaceus* (Pers.:S.F. Gray) Lloyd, *Coriolus versicolor* (L.:Fr.) Quél. and *P. sanguineus* were collected from branches of an old peach tree (*Prunus persicae* (L.) Batsch). The fruit-bodies were mainly located on the lower side but *P. sanguineus* was more abundant on

the upper side of the branches. On the base of the trunk only *Ph. pomaceus* was present. Several isolates of each species collected from peach and willow were obtained, but only one was used to provide inocula for laboratory experiments.

#### Effect of non-volatile diffusible metabolites

In order to investigate the possible involvement of non volatile diffusible metabolites in interactions, the isolates alternatively tested as metabolite producers were: *Pycnoporus sanguineus* (MVHC 5560), *Phellinus pomaceus* (MVHC 5562), and *Coriolus versicolor* (MVHC 5561) from peach; *P. sanguineus* (MVHC 5401), *T. extenuata* (MVHC 5304), *P. tigrinus* (MVHC 5400) and *L. sulphureus* (MVHC 5067) from willow. A modified version (Bettucci *et al.*, 1988) of the technique of Dennis & Webster (1971) was used. Briefly, Petri dishes of 90mm diameter containing 18ml of 2% malt-agar were used. A sterilized cellophane membrane of the same diameter was placed upon the culture medium and a disk of a fresh culture (6mm diameter) inoculated in the center. The cellophane membrane was removed 48h later. A disk of a fresh culture from other species, isolated of the same tree, was placed in the center of the culture media. Each fungus was employed as a potential antagonist. Four replicates was performed at 24 C and pH 4 at the beginning of the experiment. The diameter of each species tested was measured daily. Four replicate of each species growing on untreated culture media (control) was also performed and the diameter measured.

Growth inhibition was calculated from the formula

$$I = \frac{B.100 - 100}{T}$$

B being the mean of the diameters of the species tested with the diffusible metabolites of a potential antagonist and T the mean of the diameters of the control colonies;

Aerial and submerged mycelia from any modified mycelial organization were transferred to fresh media.

#### Interaction of dual cultures on solid media

Experimental pairings were carried on between willow wood-rotting species on one side, and between those of peach tree on the other. Four replicates of experimental pairings were made by placing disks (6mm diameter), cut from actively growing colonies, 8cm apart on 2% malt agar and incubated at 24°C in darkness, under normal atmospheric conditions. Four replicates of each species, inoculating the disk at the center of the plate, were performed under the same conditions.

Macro and micromorphological characteristics from the interaction interfaces and within 3-10mm on either side of dual cultures were observed during 6 weeks and compared with control cultures.

## RESULTS

#### Effects of non-volatile diffusible metabolite

The percentage of growth inhibitions assumed to be induced by diffusible metabolites (Table 1) generally did not exceed 15.4% in fungi from peach and 21.4% in those from willow. Although *C. versicolor* appeared to cause

100% inhibition of *Ph. pomaceus* at 48h, 12.5% inhibition was recorded 24h later, suggesting an extended lag phase before the extension of *P. pomaceus*.

Table 1. - Growth inhibition (%) at 48h of species exposed to diffusible metabolites from other species. \* The growth inhibition of *Ph. pomaceus* decreased to 12.5% at 72h. \*\* Growth stimulated.

Table 1 - Pourcentage d'inhibition de croissance d'espèces soumises aux métabolites diffusibles (à 48 heures). \* L'inhibition de croissance de *Ph. pomaceus* passe de 100% à 12.5% après 72 heures de contact. \*\* Croissance stimulée.

Metabolite producer	Strain response			
	<i>P. sanguineus</i>	<i>C. versicolor</i>	<i>Ph. pomaceus</i>	
<i>P. sanguineus</i>	-	15.4	9.1	
<i>C. versicolor</i>	1.1	-	(100) *	
<i>Ph. pomaceus</i>	10.9	7.7	-	
	<i>L. sulphur.</i>	<i>P. tigr.</i>	<i>T. exten.</i>	<i>P. sang.</i>
<i>L. sulphureus</i>	.	0	21.4	11.8
<i>P. tigrinus</i>	**	-	7.1	11.8
<i>T. extenuata</i>	**	0	-	11.8
<i>P. sanguineus</i>	**	5.0	7.1	-

Extension of *L. sulphureus* was slightly stimulated by all three other fungi tested, conversely they were generally inhibited by *L. sulphureus*.

No marked changes in developmental characteristics of the colonies were observed except when *T. extenuata* was exposed to *P. tigrinus* metabolites. *T. extenuata* produced a sterile coraloid aggregation resembling an immature frutification in the center of the colony. Sectors of prostrate alternating with farinaceous mycelium, from the irregular edges of a clear brown, cushion-like area (Figure 1b) were also produced. Aerial mycelium of the prostrate sectors, when transferred on fresh media, reverted to a normal morphology similar to that shown in Figure 1a, while the submerged mycelium of the same sector maintained the modified pattern of development, at least after five replicates.

#### Interactions of dual cultures on solid media

The outcome of interactions were deadlock, when neither fungus was able to invade the other, or replacement of one fungus by another. Recognition between the species was characterized by several modifications of hyphal morphology including: cytoplasmic degeneration, vacuolation, wall thickening and pigmentation, sporulation, profuse branching and hyphae aggregation. Pigmentation of the agar medium within or adjacent to the interaction interface frequently occurred. These outcomes are described in Table 2 and illustrated in Figure 1 (c-d).

In all dual cultures from the peach tree the reaction was deadlock.

Table 2 - Outcome and cytological modifications of interactions between wood-rotting fungi from peach (upper) and willow (bottom). C.v.: *C. versicolor*, Ph.p.: *Ph. pomaceus*, P.s.: *P. sanguineus*, P.t.: *P. tigrinus*, T.e.: *T. extenuata*, L.s.: *L. sulphureus*.

Tableau 2 - Interaction entre les champignons isolés de pêcher (partie supérieure) et de saule (partie inférieure).

<i>C. versicolor</i> P. sanguineus Deadlock. P.s. hyphae very vacuolated and plasmolysis of cytoplasm. C.v. with dense and light brown pigmented mycelium. Dark brown to black pigmentation on the agar medium at the interface and toward C.v. inocula	<i>Ph. pomaceus</i> Deadlock. P.s. as dense mat, hyphae very vacuolated and retracted cytoplasm. Ph. p. with pigmented hyphae. Light brown pigmentation on the agar medium at the interface and dark brown to black toward Ph.p. inocula.	
<i>C. versicolor</i>	Deadlock. Ph.p. pigmented thickened wall, and profusely branched hyphae. C.v. with very active cytoplasm and sinuous hyphae. Dark brown pigmentation on the agar medium at the interface.	
<i>P. sanguineus</i> T. extenuata Slight replacement of T.e by P.s. Overgrowth of P.s. mycelium with abundant arthrospores. Submerged hyphae of T.e. with vacuolated cytoplasm. Dark brown pigmentation on the agar medium at the interface and grey-green toward T.e. inocula.	<i>P. tigrinus</i> Replacement of P.t. by T.e. Brown pigmentation on the agar medium at the interface. The mycelium of T.e. raised and does not continue overgrowth when contacting the pseudo-sclerotial plate normally produced by P.t.	<i>L. sulphureus</i> Replacement of L.s. by T.e. that forms small cords in the advancing zone. L.s. growth upward and produces abundant conidia and very vacuolated hyphae. Later it is replaced by parallel organized hyphae of T.e., originated from the submerged mycelia. Clear brown pigmentation on the agar medium under the replaced mycelium.
<i>P. sanguineus</i>	Replacement of P.t. by P.s. Brown pigmentation on the interface.	Replacement of P.s. by L.s. with abundant conidia and amber-orange drops of L.s. No pigmentation on the agar medium at the interface and very light brown toward L.s. and P.s. inocula.
<i>P. tigrinus</i>		Replacement of L.s. by P.t. L.s. with abundant chlamydospores in the aerial mycelium and vacuolated, profusely branched submerged hyphae. P.t. with several vacuolated and abundant empty aerial hyphae. Parallel organization of submerged hyphae. Clear brown pigmentation on the agar medium under the replaced area of L.s.

In deadlock outcomes, the margin of *C. versicolor* and *P. sanguineus* contained sparsely branched hyaline hyphae whilst that of *P. pomaceus* consisted of a dense zone of profusely branched hyphae. In all cases the aerial mycelium adjacent to the interaction interface was raised, pigmented and denser than the remainder of the colony and from that formed in the control within the same time.

In willow the outcome was always the replacement. The organization of the marginal mycelium was different from that of the remainder of the colony. The margin of *L. sulphureus* when overgrown by *T. extenuata* and *P. tigrinus* was like that of *C. versicolor* and *P. sanguineus* in deadlock outcomes, except that it rapidly formed conidia (in front of *T. extenuata*) and chlamydospores (in front of *P. tigrinus*). The overgrowing fungi, in turn, formed aggregates of parallel hyphae in the form of small cords which subsequently converged, developing a prosenchyma upon *L. sulphureus*. When *P. sanguineus* was replaced by

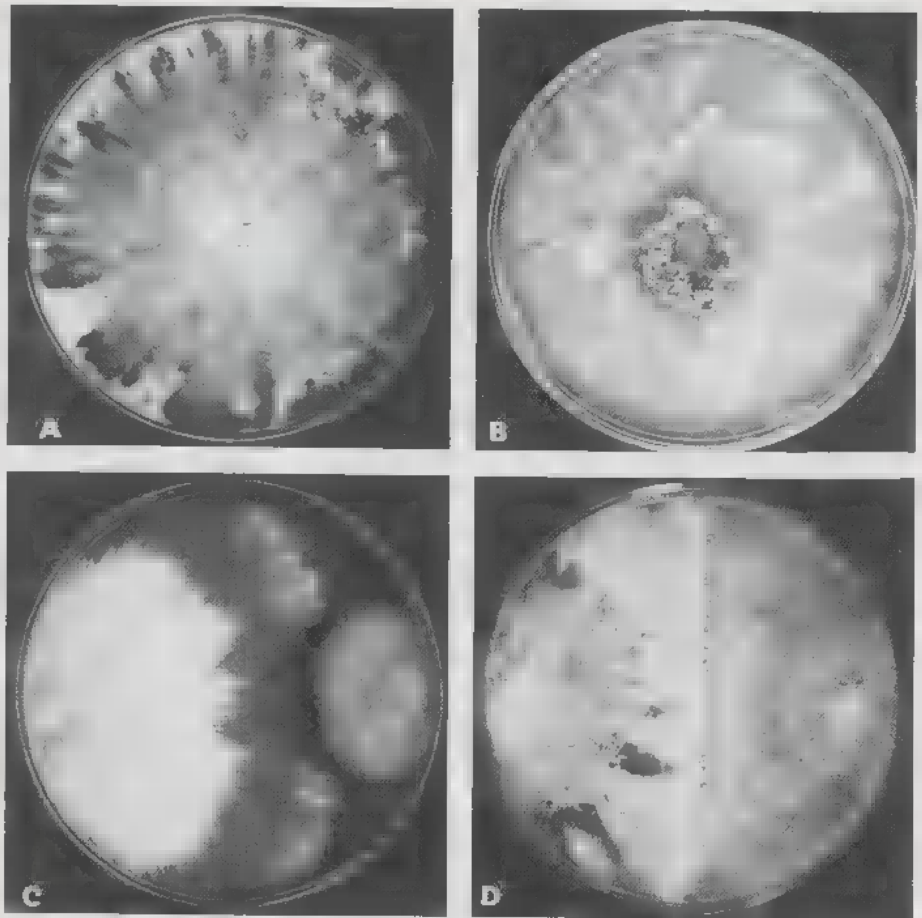


Figure 1 - Diffusible metabolites activity and outcome of interactions. Effect of diffusible metabolites of *P. tigrinus* on *T. extenuata*. (a) *T. extenuata* control. (b) *T. extenuata* treated. Morphogenetic changes induced by diffusible metabolites of *P. tigrinus*: submerged mycelium of these colonies, when transferred to fresh medium, maintained the same developmental pattern. Outcome of interactions: (c) Deadlock: *P. sanguineus* (left) and *Ph. pomaceus* (right); (d) *T. extenuata* (left) overgrowing *L. sulphureus* (right).

Figure 1 - Activité des métabolites diffusibles de *P. tigrinus* sur *T. extenuata* et interaction entre champignons. a) *T. extenuata* témoin. b) *T. extenuata* traité. Changements morphogénétiques résultant des métabolites diffusibles de *P. tigrinus* (le mycélium immergé garde le même type de développement après repiquage sur milieu frais). - Effets des interactions c) Blocage réciproque de *P. sanguineus* (à gauche) et *Ph. pomaceus* (à droite). d) Recouvrement de *L. sulphureus* par le mycélium de *T. extenuata* (à gauche).

*L. sulphureus* the margin of both mycelia were prostrated and hyaline; later both fronts coalesced and the dense, pink aerial mycelium of *P. sanguineus* behind the interface, was overgrown by *L. sulphureus*. In other cases the limit of growth was defined by dense aerial mycelium of one of the fungi, as *P. tigrinus*

or *T. extenuata* before being overgrown by *P. sanguineus*. When *T. extenuata* overgrew *P. tigrinus* dense aerial mycelium of *T. extenuata* began to form a prosenchyma replacing part of *P. tigrinus* colony. This aggregate mycelium was also formed, as described above, after transferring to fresh medium the submerged mycelium of *T. extenuata* growing in presence of diffusible metabolites of *P. tigrinus*. *T. extenuata* also formed cream-colored floccose mycelium overgrowing the remainder of the colony of *P. tigrinus* after six weeks.

## DISCUSSION

Although diffusible metabolites generally appeared to have little influence on development, the reversible modification in organization of the aerial mycelium of *T. extenuata* and the persistent changes induced in the submerged mycelium were significant. This shift in the mode of growth (Gregory, 1984) was the same as observed when *T. extenuata* was paired with *P. tigrinus*. It is possible that the metabolites responsible for these effects were of low molecular weight (as they could pass through cellophane), although in pairing experiments other molecules may be also implied (Rayner, 1986).

In replacement interactions observed between fungi of willow, overgrowing species changed their mode of growth at least three times. Probably the first trigger of change corresponded to the diffusible metabolites of *L. sulphureus*, followed by a brown pigmentation at the interface area. This pigmented zone progressively extended under the replacing mycelium. The replaced species exhibited morphogenetic, biochemical and cytological responses (as described in Table 2) implying activation of senescence mechanisms, also observed in other Basidiomycetes in presence of several different antagonist (Li, 1981; Rayner & Boddy, 1988). On the other hand, the formation of chlamydospores and conidia at the interaction interface by *L. sulphureus* (never observed in the margin of the colony of control cultures) might represent a survival mechanism before being overgrown by *P. tigrinus* or *T. extenuata*. In nature a psychogastric anamorph of *L. sulphureus* is known (Overholts, 1953).

Pigmentation of the medium was also a feature of deadlock interaction, and is a clear sign of phenoloxidase activity (Bullock, 1967; Li, 1981). Association of this activity with senescence and other developmental changes has already been proposed (Rayner & Boddy, 1988; Thompson & Rusterholz, 1982; Wessels, 1987). This might account for the growth restriction of the replaced species and the change in the mode of growth of the replacing species, as aggregate organization via products of phenoloxidase activity, may also be involved (Bullock, 1967; Miranda *et al.*, 1984; Wood, 1985).

The deadlock interactions between the species collected from peach tree might reflect partitioning in the spatial use of resources (Bradley, 1985; Moore & Hunt, 1988; Shortle & Cowling, 1978) coinciding with fruit-bodies spatial distribution.

During colonization of willow we infer that the ecological strategy of the two replacing species, *P. tigrinus* and *T. extenuata*, was to taking over domain, where *L. sulphureus* had earlier been present on the standing tree. As mycoparasitism was not observed, a non selective mechanism of antagonism could be implicated (Rayner *et al.*, 1987). In branches where *L. sulphureus* was present, *P. tigrinus* and *T. extenuata*, probably both antagonized first with *L. sulphureus*, and later between each other. In fact, after three years, *T. extenuata* dominated the court of *L. sulphureus* and of *P. tigrinus*. When *L. sulphureus* was absent *T.*

*extenuata* first superceded *P. tigrinus* but later *P. sanguineus* was the dominant population of the branches.

Although the ecological strategies of wood-rotting fungi may be modified by environmental conditions in nature (Rayner *et al.*, 1987), it may be useful to take them into account in the selection of strains for biotechnological purposes (Eriksson & Johnsrud, 1982) and for biological control purposes.

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